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Asymmetric potentials and motor effect: a large deviation approach

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Abstract

We provide a mathematical analysis of appearance of the concentrations (as Dirac masses) of the solution to a Fokker-Planck system with asymmetric potentials. This problem has been proposed as a model to describe motor proteins moving along molecular filaments. The components of the system describe the densities of the different conformations of the proteins.

Our results are based on the study of a Hamilton-Jacobi equation arising, at the zero diffusion limit, after an exponential transformation change of the phase function that rises a Hamilton-Jacobi equation. We consider different classes of conformation transitions coefficients (bounded, unbounded and locally vanishing).

Key words. Hamilton-Jacobi equations, molecular motors, Fokker-Planck equations
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1 Introduction

A striking feature of living cells is their ability to generate motion, as, for instance in muscle contraction already investigated theoretically in the 50's ([18]). But even more elementary processes allow for intra-cellular material transport along various filaments that are part of the cytoskeleton. These are known as "motor proteins". For example, myosins move along actin filaments and kinesins and dyneins move along micro-tubules. In the early 90's, it became possible to device a new generation of experiments *in vitro* where both the filaments and the motor proteins are sufficiently purified. This lead to an improved biophysical understanding of the biomotor process (see, for instance, [1, 15, 23, 11], and the tutorial book [17]) and gave rise to a large cellular biology literature. The experimental observations made possible to explain how chemical energy can be transformed into mechanical energy and to come up with mathematical models for molecular motors. The underlying principles are elementary and represent in fact the common basis for all biomotors. On the one hand, the filament provides for an asymmetric potential (this notion was introduced in the earliest theoretical descriptions by Huxley, [18]), sometimes referred to as the energy landscape. On the other hand, the protein can reach several different conformations. This can be ATP/ADP hydrolysis but five to six different states of the protein could be involved during muscular contraction.

In this paper we consider the following model: Molecules can reach I configurations with density, for each $i = 1, 2..., I$, n_i. A bath of such molecules is moving in an asymmetric potential seen differently by the I configurations denoted, for $i = 1, ..., I$, by ψ_i. Fuel consumption triggers a configuration change among the different states with rates $\nu_{ij} > 0$, for $i, j = 1, 2..., I$. Diffusion, denoted below by σ, is taken into account.

Thes simple considerations lead to the following system of elliptic equations for the densities $(n_i)_{1 \le i \le I}$:

$$\begin{cases} -\sigma \frac{\partial^2}{\partial x^2} n_i - \frac{\partial}{\partial x}(\nabla \psi_i \, n_i) + \nu_{ii} n_i = \sum_{j \neq i} \nu_{ij} n_j \qquad \text{in } (0,1), \\ \sigma \frac{\partial}{\partial x} n_i(x) + \nabla \psi_i(x) \, n_i(x) = 0 \quad \text{ for } x = 0 \text{ or } 1. \end{cases} \tag{1}$$

The zero flux boundary conditions means that the total number of molecules, in each molecular state, is preserved by transport (but not by configuration exchange).

Throughout the paper we assume that, for $i = 1, ..., I$

$$n_i > 0 \qquad \text{in } [0,1]. \tag{2}$$

The zero flux boundary condition, motivated by the additional modeling assumption that total density is conserved, leads to the condition that, for all $i = 1, ..., I$,

$$\nu_{ii} = \sum_{j,\, j \neq i} \nu_{ji}. \tag{3}$$

Several biomotor models, including the one described above, were analyzed in [7, 8, 19, 16] through optimal transportation methods. In [7] it is proved that there is a positive steady state solution that can, for instance, be normalized by

$$\int_0^1 \sum_{1 \le i \le I} n_i(x) dx = 1. \tag{4}$$

The simplest way to explain this fact is to observe that the adjoint system,

$$\begin{cases} -\sigma \frac{\partial^2}{\partial x^2} \phi_i + \nabla \psi_i \, \frac{\partial}{\partial x} \phi_i + \nu_{ii} \phi_i = \sum_{j \neq i} \nu_{ji} \phi_j \qquad \text{in } (0,1), \\ \\ \frac{\partial}{\partial x} \phi_i = 0 \quad \text{ in } \quad \{0,1\}, \end{cases} \tag{5}$$

admits the trivial solution $\phi_1 = \phi_2 = ... = \phi_I = 1$. This yields that 0 is the first eigenvalue of the system and thus of its adjoint (1). The Krein-Rutman theorem gives the n_i's, but the solution is not explicitly known except for $I = 1$, a situation where the motor effect cannot be achieved. The stability of this problem is also related to the notion of relative entropy [12, 21, 22, 20].

The typical results obtained about biomotors in [7, 16] are that, for small diffusion σ, under some precise asymmetry assumptions on the potentials, the solutions tend to concentrate, as $\sigma \to 0$, as Dirac masses at either $x = 0$ or $x = 1$. In the sequel such a behavior will be called *motor effect.*

Our results (i) provide an alternative proof of this motor effect, and (ii) allow for more general assumptions like, for instance, various scalings on the coefficients ν_{ij}. While [7, 16] transform the

system (1) into an ordinary differential equation and analyze directly its solution, here we use a direct PDE argument based on the phase functions $R_i = -\sigma \ln n_i$ that satisfy (in the viscosity sense, [2, 3, 9, 14]) a Hamilton-Jacobi solution. This is reminiscent to the method used for front propagation ([13, 4]). We recall that the appearance of Dirac concentrations in a different area of biology (trait selection in evolution theory) relies also on the phase function and the viscosity solutions to Hamilton-Jacobi equations, [10, 5].

In Section 2 we obtain new and more precise versions of the results of [7] by analyzing the asymptotics/rates as $\sigma \to 0$. In Section 3 we present new results for large transition coefficients, while in Section 4 we consider coefficients that may vanish.

2 Bounded non-vanishing transition coefficients

We begin with the assumptions on the transition rates and potentials. As far as the former are concerned we assume that

$$\text{there exists} \quad k > 0 \quad \text{such that} \quad \nu_{ij} \geq k > 0 \qquad \text{for all} \qquad i \neq j. \tag{6}$$

As far as the potentials are concerned we assume that, for all $i = 1, 2, ..., I$,

$$\psi_i \in C^{2,1}(0,1), \tag{7}$$

$$\text{there exists a finite collection of intervals} \quad (J_k)_{1 \leq k \leq M} \quad \text{such that} \quad \min_{1 \leq i \leq I} \psi_i' > 0 \quad \text{in} \quad \bigcup J_k, \tag{8}$$

and

$$\max_{1 \leq i \leq I} \psi_i' > 0 \qquad \text{in} \qquad [0,1]. \tag{9}$$

Notice that these assumptions are satisfied by periodic potentials with period $1/M$.

Figure 1: Motor effect exhibited by the parabolic system (1) with two asymmetric potentials. Left: the potentials ψ_1, ψ_2. Right: the phase functions $R_1^\sigma = -\sigma \ln(n_1^\sigma)$, $R_2^\sigma = -\sigma \ln(n_2^\sigma)$. As announced in Theorem 2.1, we have $R_1^\sigma \approx R_2^\sigma$ and are nondecreasing. This means that the densities are concentrated as Dirac masses at $x = 0$. Here we have used $\sigma = 10^{-4}$. See Figure 2 for another behavior.

Our first result is a new and more precise version of the result in [7]. It yields that the system (1) exhibits a motor effect for σ small enough and molecules are necessarily located at $x = 0$. This effect is explained by a precise asymptotic result in the limit $\sigma \to 0$.

To emphasize the dependence on the diffusion σ, in what follows we denote, for all $i = 1, ..., I$, by n_i^σ the solution of (1). Moreover, instead of (4), we use the normalization

$$\sum_{1 \leq i \leq I} n_i^\sigma(0) = 1. \tag{10}$$

We have:

Theorem 2.1 *Assume that (3), (6), (7), (8), (9) and (10) hold. Then, for all $i = 1, ..., I$,*

$$R_i^\sigma = -\sigma \ln n_i^\sigma \xrightarrow[\sigma \to 0]{} R \quad \text{in} \quad C(0,1), \quad R(0) = 0 \quad \text{and} \quad R' = \min_{1 \leq i \leq I} (\psi_i')_+ \ .$$

In physical terms, R can be seen as an effective potential for the system. To state the next result, we recall that throughout the paper we denote by δ_0 the usual δ-function at the origin.

We have:

Corollary 2.2 *Assume, in addition to (3), (6), (7), (8) and (9), that* $\min\limits_{1\le i\le I} \psi_i'(0) > 0$*, and normalize* n_i^σ *by (4) instead of (10). There exist* $(\rho_i)_{1\le i\le I}$ *such that*

$$n_i^\sigma \underset{\sigma\to 0}{\longrightarrow} \rho_i\delta_0, \quad \rho_i > 0, \quad \textit{and} \quad \sum_{1\le i\le I} \rho_i = 1.$$

There are several possible extensions of Theorem 2.1. Here we state one which, to the best of our knowledge, is not covered by any of the existing results.

To formulate it, we need to introduce the following assumption on the potentials $(\psi_i)_{1\le i\le I}$ which replaces (9) and allows to consider more general settings. It is:

$$\begin{cases} \text{the set} \quad \{x\in[0,1]:\ \max\limits_{1\le i\le I} \psi_i'(x) < 0\} \quad \text{is a union of finitely many intervals} \quad (K_l)_{1\le l\le M'}, \\ \\ \text{and} \quad (\cup J_k)^c \cap (\cup K_l)^c \quad \text{is either a finite union of intervals or isolated points.} \end{cases} \tag{11}$$

We have:

Theorem 2.3 *Assume (3), (6), (7), (8), (11) and (10). Then*

$$R_i^\sigma = -\sigma \ln n_i^\sigma \underset{\sigma\to 0}{\longrightarrow} R \quad \textit{in} \quad C(0,1), \quad R(0) = 0 \quad \textit{and}$$

$$R' = \begin{cases} \min\limits_{1\le i\le I} (\psi_i')_+ \quad \textit{in} \quad \cup J_k, \\ \\ \max\limits_{1\le i\le I} \psi_i' \quad \textit{in} \quad \cup K_l, \\ \\ 0 \quad \textit{in} \quad \mathrm{Int}\big((\cup J_k)^c \cap (\cup K_l)^c\big). \end{cases}$$

As a consequence we have:

Corollary 2.4 *In addition to (3), (6), (7), (8), (11) and (4), assume that we have the same number of intervals* J_k *and* K_l *in (8) and (11) respectively, that* 0 *is the left endpoint of* J_1 *and, finally, that, for all* $k = 1, ..., M$*,*

$$\Big|\int_{K_k} \max_{1\le i\le I} \psi_i'(y)dy\Big| < \int_{J_k} \min_{1\le i\le I} \psi_i'(y)dy.$$

Then, for all $i = 1, ..., I$*, there exist* $(\rho_i)_{1\le i\le I}$ *such that*

$$n_i^\sigma \underset{\sigma\to 0}{\longrightarrow} \rho_i\delta_0, \quad \rho_i > 0, \quad \textit{and} \quad \sum_{1\le i\le I} \rho_i = 1.$$

Other possible extensions concern coefficients that may vanish somewhere and/or be unbounded. The former case is studied in Section 4. As far as the ν_{ij} being unbounded, it will be clear from the proof of Theorem 2.1, that the coefficients can depend on σ as long as, for $\sigma \to 0$ and all $i, j = 1, ..., I$, there exists $\alpha > 0$ such that

$$\sigma \nu_{ij}^\sigma \to 0 \qquad \text{and} \qquad \sigma^{-\alpha} \nu_{ij} \to \infty.$$

Going further in this direction leads to a different limits for $-\ln n_i{}^\sigma$ that we study in the next Section.

We continue next with the proof of Theorem 2.1. The modifications needed to prove Theorem 2.3 are indicated at the end of this section where we also discuss the proofs of the Corollaries.

Proof of Theorem 2.1 A direct computation shows that the R_i^σ's satisfy, for $\widetilde{\nu}_{ii} = \nu_{ii} - \psi_i''$, the system

$$\begin{cases} -\sigma \frac{\partial^2 R_i^\sigma}{\partial x^2} + \frac{\partial R_i^\sigma}{\partial x}^2 - \psi_i'(x) \frac{\partial R_i^\sigma}{\partial x} + \sigma \sum\limits_{j=1}^{I} \nu_{ij} e^{(R_i^\sigma - R_j^\sigma)/\sigma} = \sigma \widetilde{\nu}_{ii} \quad \text{in} \quad (0,1), \\ \\ \frac{\partial R_i^\sigma}{\partial x} = \psi_i' \quad \text{in } \{0,1\}. \end{cases} \tag{12}$$

Adding the equations of (1) and using (3) yield the conservation law

$$-\sigma \frac{\partial^2}{\partial x^2} [\sum_{1 \le i \le I} n_i^\sigma] - \frac{\partial}{\partial x} [\sum_{1 \le i \le I} \psi_i' n_i^\sigma] = 0,$$

which together with the boundary condition gives

$$-\sigma \frac{\partial}{\partial x} \sum_{1 \le i \le I} n_i^\sigma - \sum_{1 \le i \le I} \psi_i' n_i^\sigma = 0. \tag{13}$$

Setting

$$\sum_{1 \le i \le I} n_i^\sigma = e^{-S^\sigma/\sigma},$$

we have

$$\frac{\partial S^\sigma}{\partial x} = \frac{\sum_i \psi_i' n_i^\sigma}{\sum_i n_i^\sigma},$$

and, as a consequence, the *total flux estimate*

$$\min_{1 \le i \le I} \psi_i' \le \frac{\partial S^\sigma}{\partial x} \le \max_{1 \le i \le I} \psi_i'. \tag{14}$$

The normalization (10) of the n_i^σ's implies that $S^\sigma(0) = 0$. As a result, there exists a $S \in C^{0,1}(0,1)$ such that, after extracting a subsequence,

$$\begin{cases} S^\sigma \xrightarrow[\sigma \to 0]{} S, \qquad S(0) = 0, \qquad \text{and} \\ \\ \min\limits_{1 \le i \le I} \psi_i' \le \frac{\partial S}{\partial x} \le \max\limits_{1 \le i \le I} \psi_i' \quad \text{in } [0,1]. \end{cases} \tag{15}$$

Next we obtain bounds on the R_i^σ's, which are independent of σ, and imply their convergence as $\sigma \to 0$. This is the topic of the next Lemma which we prove after the end of the ongoing proof.

Lemma 2.5 *For each $i = 1, ..., I$ there exists a positive constant $C_i = C_i(\psi_i', \sigma\nu_{ii}, \sigma\psi_i''))$ such that*

$$|R_i^\sigma| + |\frac{\partial R_i^\sigma}{\partial x}| \le C_i \quad \text{in} \quad [0,1],$$

Moreover, for all $i = 1, ..., I$,

$$R_i^\sigma \xrightarrow[\sigma\to 0]{} R = S, \qquad \text{in } C([0,1]).$$

We obtain next the Hamilton-Jacobi satisfied by the limit $R = S$. The claim is that the limit is a viscosity solution (see, for instance, [3, 9]) of

$$\left|\frac{\partial R}{\partial x}\right|^2 + \max_{1\le i\le I}[-\psi_i'\frac{\partial R}{\partial x}] = 0 \qquad \text{in} \quad (0,1). \tag{16}$$

We do not state the boundary condition because we do not use them. It can, however, be proved that R satisfies

$$\frac{\partial R}{\partial x} \le \max_{1\le i\le I}\psi_i' \quad \text{at} \quad x=0 \quad \text{and} \quad \frac{\partial R}{\partial x} \ge \min_{1\le i\le I}\psi_i' \quad \text{at} \quad x=1.$$

We begin with the subsolution property. Letting $\sigma \to 0$ in the inequality

$$-\sigma\frac{\partial^2 R_i^\sigma}{\partial x^2} + \left|\frac{\partial R_i^\sigma}{\partial x}\right|^2 - \psi_i'\frac{\partial R_i^\sigma}{\partial x} \le \sigma\widetilde{\nu}_{ii},$$

gives, for all $i = 1, ..., I$,

$$\left|\frac{\partial R}{\partial x}\right|^2 - \psi_i'\frac{\partial R}{\partial x} \le 0.$$

To prove that R is a supersolution of (16) we observe that function $R^\sigma = \min_{1\le i\le I} R_i^\sigma$ satisfies the inequality

$$-\sigma\frac{\partial^2 R^\sigma}{\partial x^2} + \left|\frac{\partial R^\sigma}{\partial x}\right|^2 + \max_{1\le i\le I}[-\psi_i'(x)\frac{\partial R^\sigma}{\partial x}] + \sigma\sum_{i,j=1}^{I}\nu_{ij} \ge \sigma\min_i(\widetilde{\nu}_{ii}).$$

Letting again $\sigma \to 0$, we find that $R = S = \lim_{\sigma\to 0} R^\sigma$ satisfies

$$\left|\frac{\partial R}{\partial x}\right|^2 + \max_{1\le i\le I}[-\psi_i'(x)\frac{\partial R}{\partial x}] \ge 0.$$

We obtain now the formula for R. To this end, observe first that, since $\lim_{\sigma\to 0} R^\sigma = R = S$, letting $\sigma \to 0$ in (14) yields

$$\min_{1\le i\le I}\psi_i' \le \frac{\partial R}{\partial x} \le \max_{1\le i\le I}\psi_i'. \tag{17}$$

Next we show that, in the viscosity sense,

$$\frac{\partial R}{\partial x} \ge 0. \tag{18}$$

Indeed for a test function Φ, let $x_0 \in (0,1)$ be the maximum of $R-\Phi$, i.e., $(R-\Phi)(x_0) = \max\limits_{0\le x\le 1}(R-\Phi)(x)$ and assume that

$$\Phi'(x_0) < 0.$$

Applying the viscosity subsolution criterion to (17), then implies that

$$\Phi'(x_0) - \max_i \psi_i'(x_0) \ge 0.$$

This, however, contradicts the inequality

$$\max_{1\le i\le I} \psi_i'(x_0) > 0$$

that follows from the assumption (8).

Combining (17) and (18) we get

$$\min_{1\le i\le I} (\psi_i')_+ \le \frac{\partial R}{\partial x} \le \max_{1\le i\le I} \psi_i'. \tag{19}$$

Finally, given a test function Φ, let $x_0 \in (0,1)$ be such that $(R-\Phi)(x_0) = \max\limits_{0\le x\le 1}(R-\Phi)$ and assume that

$$\Phi'(x_0) > 0.$$

Again by the viscosity criterion we must have

$$\Phi'(x_0) - \min_{1\le i\le I} \psi_i'(x_0) \le 0,$$

and, hence, in the viscosity sense,

$$\frac{\partial R}{\partial x} \le (\min_{1\le i\le I} \psi_i')_+ \qquad \text{if } \frac{\partial R}{\partial x} > 0. \tag{20}$$

This concludes the proof of the formula in the claim. $\square$

We return now to the

Proof of Lemma 3.1 For the Lipschitz estimate, observe that, at any extremum point x_0 of $\frac{\partial R_i^\sigma}{\partial x}$, we have $\frac{\partial^2 R_i^\sigma}{\partial x^2} = 0$. Evaluating the equation at x_0, we get

$$\left|\frac{\partial R_i^\sigma}{\partial x}\right|^2 \le \psi_i' \frac{\partial R_i^\sigma}{\partial x} + \sigma \widetilde{\nu}_{ii}.$$

As a consequence, at x_0 we have

$$\left|\frac{\partial R_i^\sigma}{\partial x}\right| \le \max_{0\le x\le 1} \psi_i' + \sqrt{\sigma \widetilde{\nu}_{ii}}.$$

To identify the limit of $\min_{1\le j\le I} R_j^\sigma$ notice that the inequality

$$n_i^\sigma \le \sum_{1\le j\le I} n_j^\sigma \le I \max_j n_j^\sigma$$

gives

$$-\sigma \ln I + \min_{1\leq j\leq I} R_j^\sigma \leq S^\sigma \leq R_i^\sigma,$$

and thus

$$S^\sigma \leq \min_{1\leq i\leq I} R_i^\sigma.$$

Consequently, we have the uniform convergence

$$\min_{1\leq i\leq I} R_i^\sigma \xrightarrow[\sigma\to 0]{} S.$$

To prove the claim about the limit of the R_i^σ we observe that summing over i the equations of (12) yields

$$\sigma \sum_{i,j=1}^{I} \nu_{ij} (\frac{(R_j^\sigma - R_i^\sigma)_+}{\sigma})^2 \leq 2\sigma \sum_{i,j=1}^{I} \nu_{ij} e^{(R_i^\sigma - R_j^\sigma)/\sigma} \leq 2(\sigma \sum_{1\leq i\leq I} \widetilde{\nu}_{ii} + 2\sigma \frac{\partial^2 \sum_i R_i^\sigma}{\partial x^2} + \sum_{1\leq i\leq I} \psi_i' \frac{\partial R_i^\sigma}{\partial x}).$$

Integrating in x and using the gradient estimates, we find that

$$\sum_{i,j=1}^{I} \int_0^1 (R_j^\sigma - R_i^\sigma)^2 = \frac{1}{2} \sum_{i,j=1}^{I} \int_0^1 (R_j^\sigma - R_i^\sigma)_+^2 \leq C\sigma.$$

Together with the uniform gradient estimate on R_i^σ and the uniform bound on $\min_{1\leq j\leq I} R_j^\sigma$, we deduce that

$$R_i^\sigma \xrightarrow[\sigma\to 0]{} R = S \in C^{0,1}(0,1).$$

□

We continue with the

Proof of Corollary 2.2 The normalization (4) amounts to adding a constant to the R_i. The exponential behavior of n_i^σ, with an increasing R_i^σ (from Theorem 2.1), yields that the n_i^σ's converge, as $\sigma \to 0$, to 0 uniformly on intervals $[\varepsilon, 1]$ with $\varepsilon > 0$. Moreover, $R(0) = 0$. The result follows with $\rho_i \geq 0$. If $\rho_i = 0$ for some $i = 1, ..., I$, then, letting $\sigma \to 0$ in (1), gives, in the sense of distributions, that

$$0 = \sum_{j\neq i} \nu_{ij} n_j.$$

But then all the ρ_j must vanish, which is impossible with the normalization of unit mass. □

We present now a brief sketch of the proof of Theorem 2.3. Since it follows along the lines of the proof of Theorem 2.1, here we only point out the differences.

We have:

Proof of Theorem 2.3 The Lipschitz estimates, the passage in the limit and the identification of the limiting Hamilton-Jacobi equation in the Theorem 2.1 did not depend on the assumption (9), hence, they hold true also on the case at hand. The final arguments of the proof of Theorem 2.3 also identify the limit on the set $(\cup K_l)^c$. On the set $\cup K_l$ we already know from (17) that R' is less than the claimed value, and thus it is negative. We conclude the equality by using the Hamilton-Jacobi equation. Indeed in this situation we know that

$$\max_{1\leq i\leq I} [-\psi_i' \frac{\partial R}{\partial x}] = -\frac{\partial R}{\partial x} \max_{1\leq i\leq I} \psi_i'.$$

□

We conclude the section with the proof Corollary 2.4, which is simply a variant of the one for Corollary 2.2. We have:

Proof of Corollary 2.4 The assumption on $\cup J$ asserts that R is increasing on $\cup J$. Then it may decrease but, for $x > 0$, $R(x) > R(0)$. With the unit mass normalization, this means that $R(0) = 0$ as before and the convergence result holds as before. □

3 Large transition coefficients

Figure 2: MOTOR EFFECT EXHIBITED BY THE PARABOLIC SYSTEM (21) WITH LARGE TRANSITION COEFFICIENTS. THE FIGURE DEPICTS THE PHASE FUNCTIONS R_1^σ, R_2^σ. AS ANNOUNCED IN THEOREM 3.1, WE HAVE $R_1^\sigma \approx R_2^\sigma$ AND CAN DECREASE SLIGHTLY. HERE WE HAVE USED $\sigma = 5\ 10^{-3}$.

In this section we consider transition coefficients normalized by $1/\sigma$. For the sake of simplicity we take $I = 2$. This allows for explicit formulae. The equations for larger systems, i.e., $I > 3$, are more abstract. The system (1) is replaced by

$$\begin{cases} -\sigma \frac{\partial^2}{\partial x^2} n_1^\sigma - \frac{\partial}{\partial x}(\nabla\psi_1\ n_1^\sigma) + \frac{1}{\sigma}\nu_1 n_1^\sigma = \frac{1}{\sigma}\nu_2 n_2^\sigma \quad \text{in} \quad (0,1), \\ \\ -\sigma \frac{\partial^2}{\partial x^2} n_2^\sigma - \frac{\partial}{\partial x}(\nabla\psi_2\ n_2^\sigma) + \frac{1}{\sigma}\nu_2 n_2^\sigma = \frac{1}{\sigma}\nu_1 n_1^\sigma \quad \text{in} \quad (0,1), \\ \\ \sigma \frac{\partial}{\partial x} n_i^\sigma + \nabla\psi_i\ n_i^\sigma = 0 \quad \text{in} \quad \{0,1\} \quad \text{for} \quad i = 1,2. \end{cases} \tag{21}$$

As before we assume that

$$n_i^\sigma > 0 \quad \text{in } [0,1] \quad \text{for} \quad i = 1,2. \tag{22}$$

The result is:

Theorem 3.1 *Assume (3), (6), (7), (8) and (9) and consider the solution (n_1^σ, n_2^σ) to (21) normalized by $n_1^\sigma(0) + n_2^\sigma(0) = 1$. Then, as $\sigma \to 0$ and $i = 1,2$,*

$$R_i^\sigma = -\sigma \ln n_i^\sigma \underset{\sigma \to 0}{\longrightarrow} R \quad \textit{in } C(0,1), \qquad R(0) = 0, \quad \textit{and}$$

$$R' \geq \begin{cases} \min\limits_{1 \leq i \leq I} \psi_i' & \textit{on } \ \cup J_l, \\ \\ -\sqrt{k} & \textit{on } \ (\cup J_l)^c. \end{cases}$$

The corollary below follows from Theorem 3.1 in a way similar to the analogous corollaries in the previous section. Hence, we leave the details to the reader.

Corollary 3.2 *In addition to the assumptions of Theorem 3.1, suppose that $0 \in J_1$, the potentials are small enough so that*

$$\sqrt{k}\ |K| < \int_{\sup J} \min_{1 \leq i \leq 2} \psi_i'(y) dy,$$

and (n_1^σ, n_2^σ) *is normalized by (4). There exist* $\rho_1, \rho_2 > 0$ *such that* $\rho_1 + \rho_2 = 1$ *and, as* $\sigma \to 0$ *and for* $i = 1, 2$,

$$n_i^\sigma \xrightarrow[\sigma \to 0]{} \rho_i \delta_0.$$

We present next a sketch of the proof of Theorem 3.1 as most of the details follow as in the previous theorems.

Proof of Theorem 3.1 The total flux and Lipschitz estimates follow as before. The main new point is the limiting Hamilton-Jacobi equation which is more complex. We formulate this as a separate lemma below. Its proof is based on the use of perturbed test functions. We refer to [4] for the rigorous argument in a more general setting.

Lemma 3.3 *The uniform in* $[0, 1]$ *limit* R*, as* $\sigma \to 0$*, of the* R_i^σ *satisfies the Hamilton-Jacobi equation*

$$H\left(\frac{\partial R}{\partial x}, x\right) = 0, \qquad in \qquad (0, 1) \tag{23}$$

with

$$H(p, x) = \frac{1}{2}[\beta_1 + \beta_2 + \sqrt{(\beta_1 + \beta_2)^2 - 4(\beta_1\beta_2 - \nu_1\nu_2)}], \tag{24}$$

where, for $i = 1, 2$,

$$\beta_i = p^2 - \psi_i'\, p - \nu_i.$$

The formula for R' follows from the above Lemma by analyzing the solutions to the Hamilton-Jacobi equation as before. On the set $\cup J_l$ the answer follows from the bounds (14). On the set $(\cup J)^c$ the argument is more elaborate. Using that R' is a subsolution, we get

$$\beta_1\beta_2 - \nu_1\nu_2 \geq 0 \quad \text{and} \quad \beta_1 + \beta_2 \leq 0.$$

Therefore both β_1 and β_2 are nonpositive and thus

$$(R')^2 - \psi_i' R' - \nu_i \leq 0.$$

On the other hand we know that on $(\cup J_l)^c$ one of the potentials – for definiteness say ψ_1 – satisfies $\psi_1' > 0$, hence, always in $(\cup J_l)^c$,

$$R' \geq \frac{1}{2}[\psi_1'(x) - \sqrt{(\psi_1')^2 + 4\nu_1}] \geq \sqrt{\nu_1}.$$

The inequalities for R' are now proved. □

4 Vanishing transition coefficients

We focus here to the case where the transition coefficients $(\nu_{ij})_{1 \leq i,j \leq I}$ may vanish at either some points or, in fact, on large sets. In this situation, we assume that

$$\begin{cases} \text{for each } j = 1, ..., I, \quad \psi_j' < 0 \quad \text{on a finite collection of intervals} \quad (K_j^\alpha)_{1 \leq \alpha \leq A_j} \quad \text{and} \\ \text{for all } j = 1, ..., I \text{ and } \alpha = 1, ..., A_j, \text{ there exists } i \in \{= 1, ..., I\} \text{ such that} \\ \psi_i' \geq 0 \text{ on } K_j^\alpha, \quad \text{and, in a left neighborhood of the right endpoint of } K_j^\alpha, \quad \nu_{ij} > 0. \end{cases} \tag{25}$$

To go for weaker assumptions would face the completely decoupled case (when ν vanishes) and the motor effect does not occur.

We have:

Theorem 4.1 *Assume (7),(8),(9), (25) and normalize the solution $(n_i^\sigma)_{1\leq i\leq I}$ to (21) by (10). For $i=1,...,I$, let $R_i^\sigma = -\ln n_i^\sigma$. Then, as $\sigma \to 0$,*

$$\text{either} \quad R_i^\sigma \xrightarrow[\sigma\to 0]{} R_i \quad \text{in } C(0,1), \qquad \text{or} \quad R_i^\sigma \xrightarrow[\sigma\to 0]{} \infty \quad \text{uniformly in} \quad [0,1].$$

Moreover, the function $R = \min\limits_{1\leq i\leq I} R_i$ satisfies

$$R(0) = 0, \quad R' \geq 0 \quad \text{and} \quad R' = \min_{1\leq i\leq I} \psi_i' \quad \text{on} \quad \cup J_l.$$

We also have:

Corollary 4.2 *In addition to the assumptions of Theorem 4.1, suppose that $0 \in J_1$. For $i = 1,,,I$, there exist $\rho_i \geq 0$ such that $\sum_{1\leq i\leq I}\rho_i = 1$, and, as $\sigma \to 0$,*

$$n_i^\sigma \xrightarrow[\sigma\to 0]{} \rho_i\delta_0.$$

The direct conclusion of Theorem 4.1 is simply that

$$\sum_{1\leq i\leq I} n_i^\sigma \xrightarrow[\sigma\to 0]{} \delta_0$$

.

The corollary follows from the fact that, for all $i=1,...,I$, $n_i^\sigma \geq 0$. We do not know whether in this context each ρ_i is positive. To get this, we need to assume something more like, for example, $\nu_{ij}(0) > 0$ for all $i,j = 1,...,I$.

We conclude with a brief sketch of the

Proof of Theorem 4.1. The total flux and Lipschitz estimates follow as before. A careful look at the proof of the convergence part of Theorem 2.1 shows that either the R_i^σ's blow up or they are uniformly bounded and, hence, converge uniformly in $(0,1)$ to a subsolution of

$$|R_i'|^2 - \psi_i' R_i' \leq 0.$$

It then follows that

$$R_i' \geq 0 \text{ on } (\cup_\alpha K_i^\alpha)^c \quad \text{and } R_i' \leq \psi_i'(x) \text{ on } \cup_\alpha K_i^\alpha.$$

The final step is to prove that

$$R(x) = \min_{i\in L(x)} R_i(x) \quad \text{in} \quad L(x) = \{i,\ \psi_i'(x) \geq 0\}.$$

This follows as before. We leave the details to the reader. □

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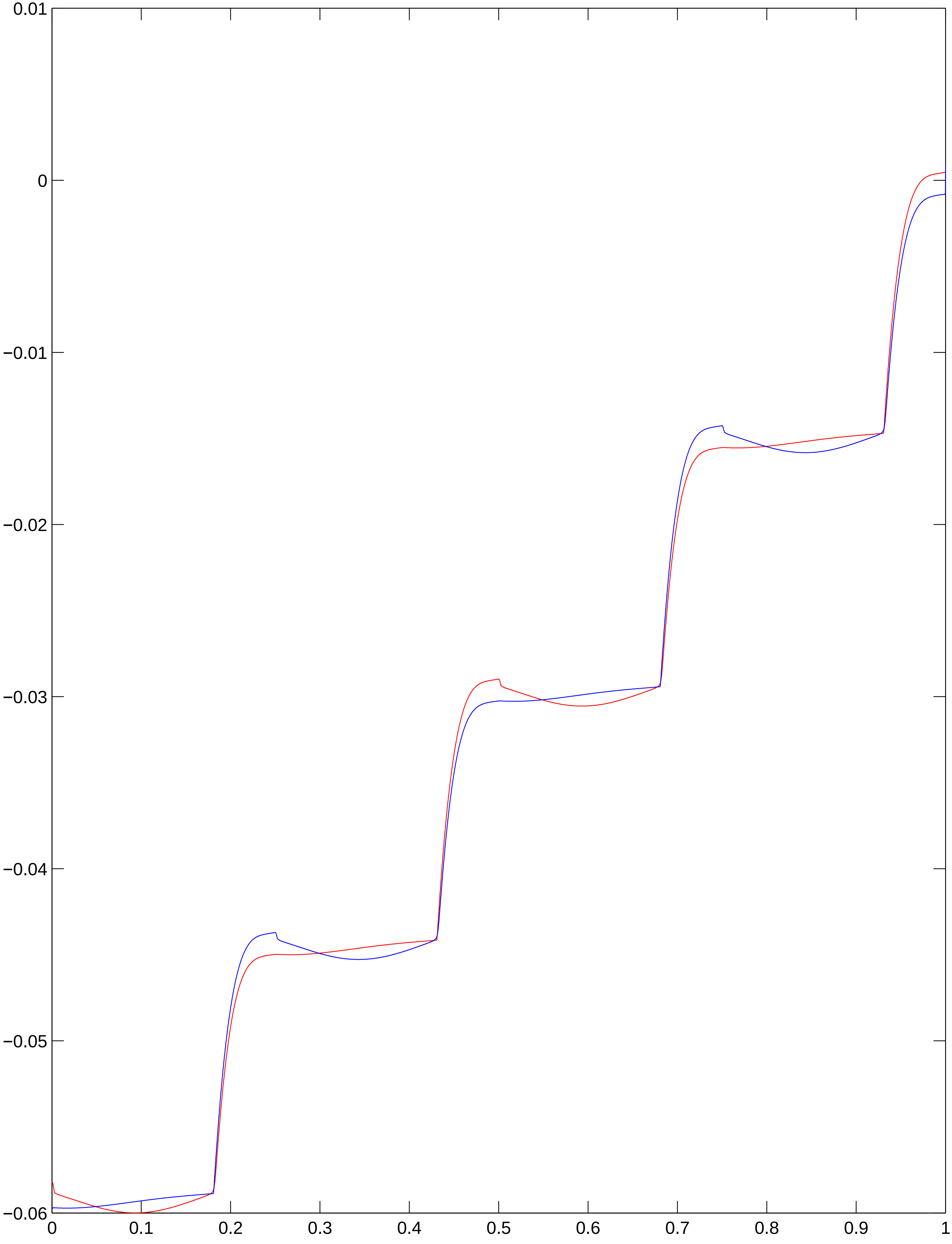
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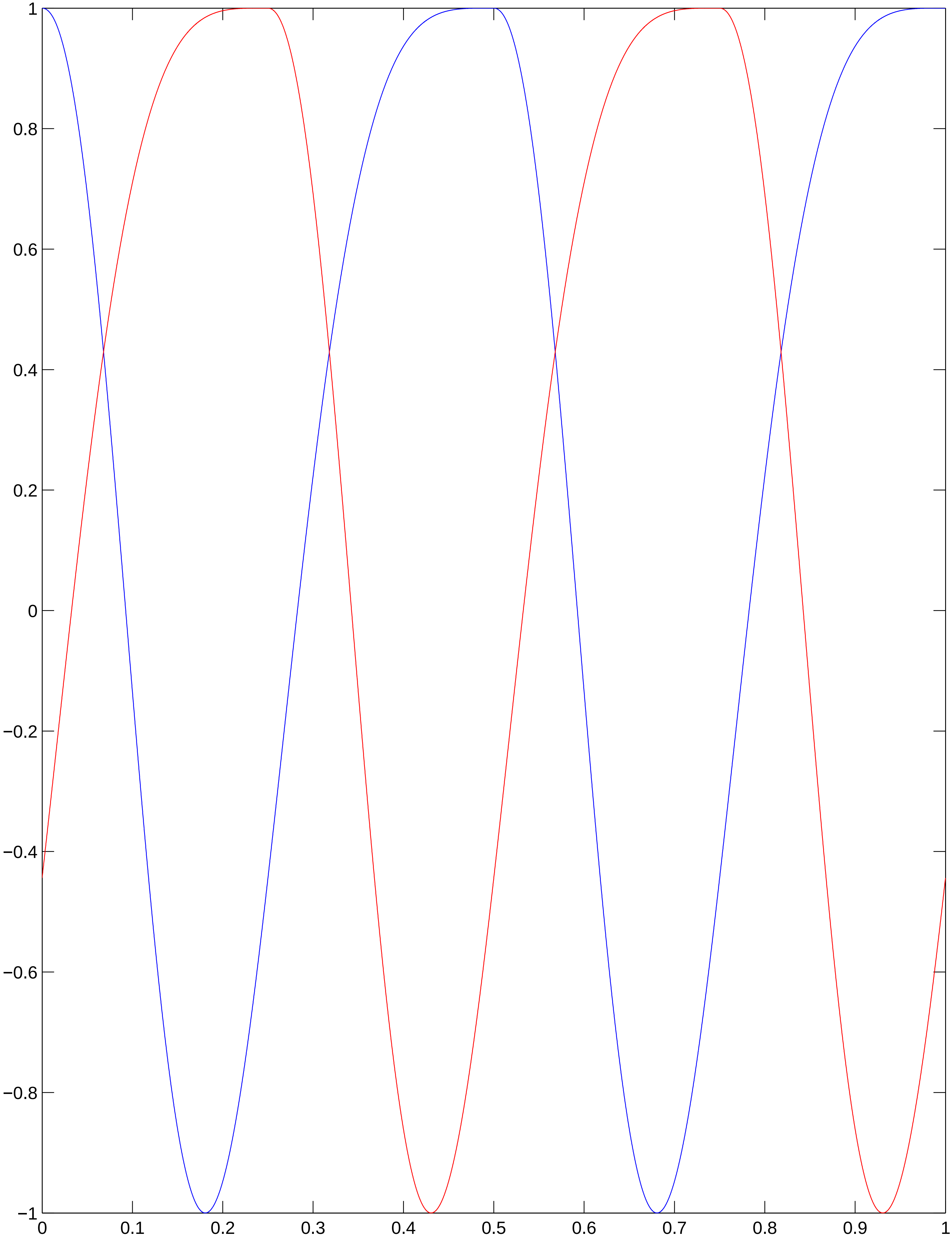
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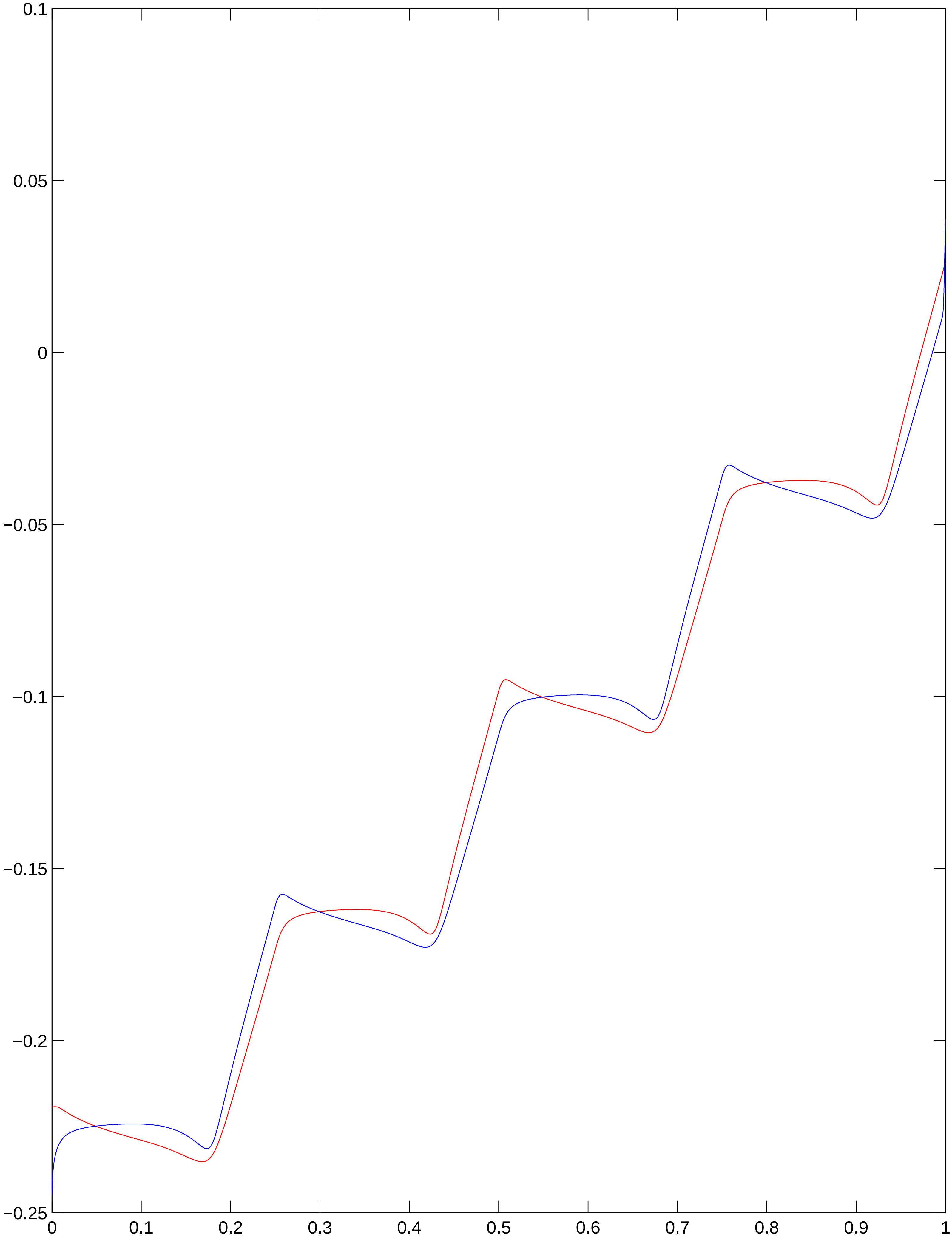
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